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# First Record of Pterosaurs from the Early Cretaceous Tetori Group: a Wing-phalange from the Amagodani Formation in Shokawa, Gifu Prefecture, Japan

By

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**Abstract** We report on the first pterosaur from the Tetori Group of Central Honshu, Japan. It was found in the non-marine Early Cretaceous Amagodani Formation, Shokawa, Gifu Prefecture. An incomplete proximal wing-phalange is assigned to Dsungaripteridae gen. et sp. indet. The bone is relatively thick-walled for a pterosaur: the ratio of the internal to external diameter (K), is approximately 0.55. This might have been an adaptation for reducing the risk of breakage or for thermal soaring over land.

## Introduction

In August, 1994, an almost complete pterosaur wing-phalange was found in the Early Cretaceous Amagodani Formation at Shokawa Village in Gifu Prefecture, Honshu, by one of us (KS). Originally, K. SHIMIZU noticed a hollow bone visible in cross section, in a fine-grained sandstone block found at the foot of a cliff where the Gifu-Ken Dinosaur Research Committee had been prospecting for dinosaur fossils in 1992–1995 (Fig. 1: Grid reference=36°02′30″N, 136°53′30″E). The sandstone is thought to come from a section in the lower part of the Amagodani Formation, exposed in the outcrop above. SHIMIZU recovered the block and prepared out the specimen. It proved to be a long hollow bone with no articular end. SHIMIZU thought that it belonged to a pterosaur, or bird, because it was hollower than other bones he had seen from the Tetori Group.

In October, 1994, SHIMIZU showed the specimen to D. UNWIN who was visiting Japan for two weeks in order to study pterosaur materials in Japanese collections. UNWIN suggested that it was most likely to be a pterosaurian wing-phalange, possibly of a dsungaripterid. SHIMIZU later prepared out an

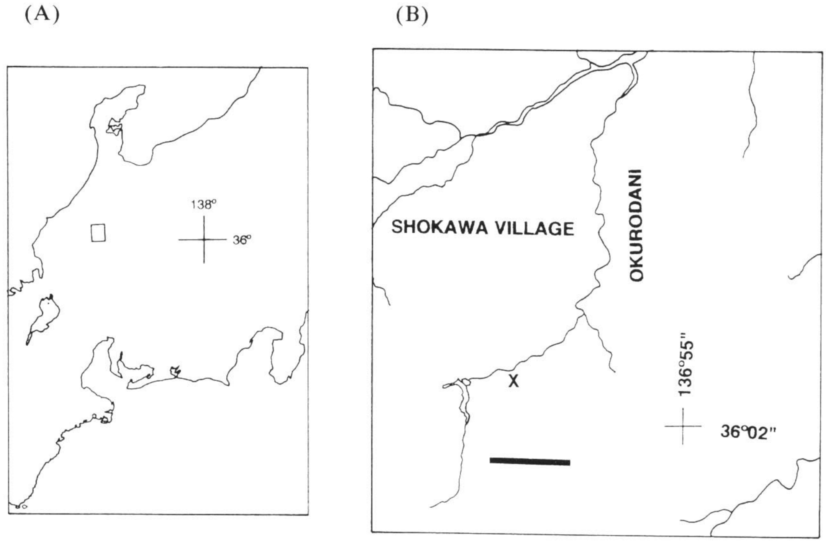


Fig. 1. A, Island of Honshu, with location of detailed map. B, Location map. The locality is marked X on this map which only otherwise indicates the water system, traced from the 1:25,000-scale Geographical Survey Institute Topographical Map of Arabuchi. Scale bar is 500 m.

articular end of the bone, which was still in the matrix when UNWIN first saw the specimen. UNWIN subsequently confirmed the specimen as an incomplete first or second wing-phalange of a dsungaripterid. In the summer of 1995, three of us (DMU, MM, and YH) met in Beijing on the occasion of the Sixth Mesozoic Ecosystem Symposium and confirmed this identification by comparison with the dsungaripterid material in the care of Professor Zhiming DONG, Institute of Vertebrate Palaeontology and Palaeoanthropology, Academica Sinica.

This is the first pterosaur specimen from the Tetori Group and only the third pterosaur to be described from the Japanese Archipelago. The first was a partial limb bone, thought to belong to *Pteranodon* sp. (NSM PV15005) from the IIId section of the Upper Yezo Group (Santonian-Lower Campanian) in Mikasa, Hokkaido (OBATA *et al.*, 1972). The second was a first wing-finger phalange only identifiable as pterodactyloid from the Mifune Group (Upper Cenomanian-Turonian) in Mifune, Kumamoto, Kyushu (OKAZAKI & KITAMURA, 1996). Although only three pterosaur specimens have been described in Japan so far, more specimens have been found in Hokkaido (Ren HIRAYAMA, personal communication, 1996) and in Kyushu, including a fragmentary cranial crest from the Santonian section of the Himenoura Group in Kumamoto, Kyushu (OKAZAKI, 1995).

## Abbreviation

NSM National Science Museum, Tokyo, Japan.

## Geological Setting

The geology of the locality has been reported in detail elsewhere, following intensive prospecting for dinosaurs by the Gifu Prefectural Museum (e.g. GIFU-KEN DINOSAUR RESEARCH COMMITTEE, 1993, 1994). The fine-grained sandstone block that contained the pterosaur specimen is believed to be from the lowermost part of the Amagodani Formation, which is likely to be Hauterivian-Barremian in age, as the underlying Okurodani Formation is dated at $135 \pm 7$ Ma based upon fission-track dating of tuffs (GIFU-KEN DINOSAUR RESEARCH COMMITTEE, 1993). The Amagodani Formation consists of alternating beds of mudstone and fine-grained sandstone with a channel-shaped sandstone bed at Shokawa. This locality has also produced iguanodontid teeth and unidentifiable bone fragments of fishes, turtles, and other reptiles (e.g. HASEGAWA *et al.*, 1995; GIFU-KEN DINOSAUR RESEARCH COMMITTEE, 1993).

## Systematic Palaeontology

Class Reptilia LINNAEUS, 1758

Subclass Diaspida OSBORN, 1903

Order Pterosauria OWEN, 1840 (KAUP, 1834)

Suborder Pterodactyloidea PLIENINGER, 1901

Family Dsungaripteridae YOUNG, 1964

Dsungaripteridae gen. et sp. indet.

*Diagnosis*: The elongate, dorso-ventrally compressed, spar-like phalange, with straight or gently curved profiles and terminal articular surface is easily identifiable as pterosaur. The characters indicative of Dsungaripteridae include slight forward reflection, thick bone walls, and an expanded articular surface.

*Material*: A partial left proximal wing-phalange (NSM PV20042).

*Description*: The bone, composed of three contiguous fragments, consists of an almost complete wing-phalange lacking the proximal end (Fig. 2). Judging by its very gentle dihedral this phalange was from the left wing-finger. As preserved, the phalange is 82.5 mm in length and, when complete, had a minimum length of at least 90 mm (Fig. 3). The bone is hollow, but for a pterosaur, has relatively thick bone walls forming approximately 55% of the total cross-sectional diameter. The average value for K, the ratio of the internal to the external diameter


Fig. 2. Left proximal wing-phalange of dsungaripterid from Shokawa, Gifu Prefecture, Japan (NSM PV20042), in (A) distal, (B) dorsal, (C) ventral, and (D) posterior view. Scale bar = 5 mm.

Fig. 3. Reconstruction of the left proximal wing-phalange in ventral view. This restoration is based on the proximal wing-phalange of *Santanadactylus pricei* (WELLENHOFER, 1991: 86).

(CURREY & ALEXANDER, 1985), is 0.55 and, for R/t, the ratio of the bone wall thickness to the radius of the bone (CURREY & ALEXANDER, 1985) is 2.26. Proximally, the bone shaft is uncrushed and has a flattened-oval cross-section. Distally, the shaft has been dorso-ventrally compressed, and the bone walls have collapsed inward, resulting in a deep, longitudinal groove in the dorsal surface and a shallower groove in the ventral surface. The surface of the bone shaft bears a fine, longitudinal lineation (Fig. 4). This also occurs in other pterosaurs and is particularly well developed in the late Jurassic rhamphorhynchoid *Sordes pilosus.*

The distal end of the phalange bears a well developed articular condyle, gently convex from dorsal to ventral and rather more convex from anterior to posterior. In terminal aspect the condyle has an irregular, boot-shaped outline, the more acute 'heel end' toward the anterior, the more obtuse 'toe end' toward the posterior. Unlike most pterosaurs, wherein the articular region is continuous with the bone shaft, the condyle is somewhat expanded, and projects beyond the

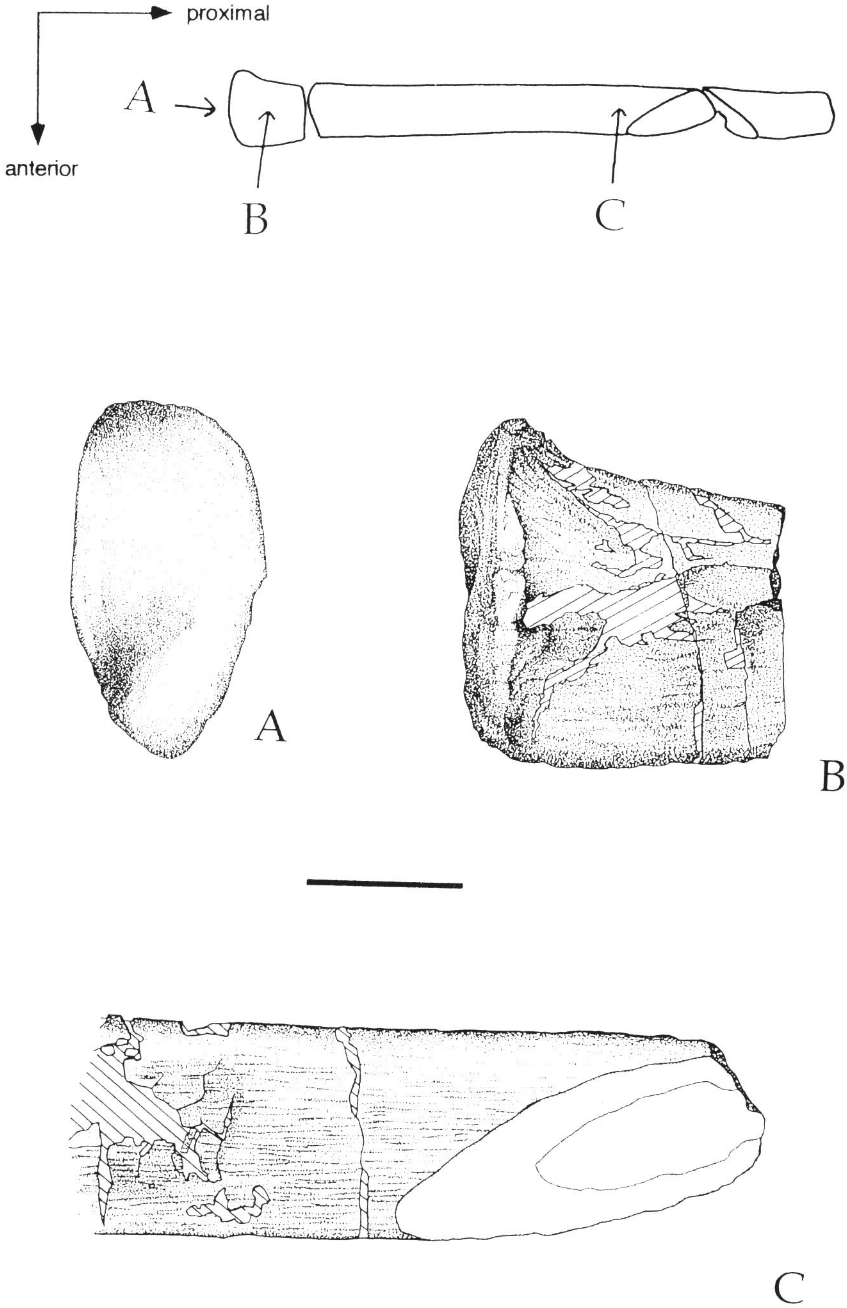


Fig. 4. Details of NSM PV20042, with anterior to the bottom and distal to the left of the figure. A, distal view of the articular condyle; B, ventral view of the condyle; and C, ventral view of the mid-shaft region where a break shows the oblique cross-section of the bone and the thick bone walls. Scale bar = 5 mm.

margins of the shaft. This is most clearly seen in ventral and anterior aspect and further accentuated by crushing. The margins of the condyle are roughened, indicating attachment sites for the collateral ligaments.

In dorsal aspect the phalange has a somewhat unusual outline. Typically, phalanges curve backward, and have a convex anterior profile (e.g. WELLNHOFER, 1991, fig 33a). In this case, the phalange curves somewhat forward (=rostral reflection) and has a gently concave anterior profile. Rostral reflection of the first wing-phalange occurs in a number of pterosaurs, including dsungaripteroids and, though less pronounced, also appears in the second wing-phalange. The degree of curvature exhibited by the Shokawa specimen suggests that it is most probably a first wing-phalange.

The hyper-elongation of the fourth digit to form a wing-finger is unique to pterosaurs (WELLNHOFER, 1978). The elongate, dorso-ventrally compressed, spar-like wing-finger phalanges, with straight or gently curved profiles and terminal articular surfaces are easily identifiable and diagnostic of pterosaurs. The Shokawa phalange corresponds in all respects to the wing-phalanges of pterosaurs and is undoubtedly pterosaurian.

Despite their relative simplicity, wing-phalanges exhibit some morphological variation. For example, the cross-section can be c-shaped (WELLNHOFER, 1975) sub-triangular (WELLNHOFER, 1985, 1991), or even 'T-shaped' (BENNETT, 1994). These and other features can be tied to particular clades, but are usually only diagnostic at very general taxonomic levels. The most important feature of the Shokawa specimen is its forward curvature. Among Lower Cretaceous pterosaurs this particular shape is only found among dsungaripterids, a family of medium-sized to large, crested pterodactyloids currently only certainly recorded from Asia. This identification is further supported by the presence of unusually thick bone walls, which seem to be a typical feature of dsungaripterids (UNWIN, 1988). Expansion of the articular ends of the wing-phalanges is also a feature of some dsungaripterids, but is not diagnostic of this family, as it also occurs in non-dsungaripterids.

Dsungaripterids include: *Dsungaripterus* and *Noripterus* from the Lower Cretaceous of China (YOUNG, 1964, 1973); and '*Phobetor*' from the Lower Cretaceous of Mongolia (BAKHURINA 1982, 1986, 1993; BAKHURINA & UNWIN, 1995). *Dsungaripterus*-like material has also been reported from Romania (JURCSÁK & POPA, 1984), but the identity of this material has yet to be confirmed. BENNETT (1989, 1994) has argued that material of *"Santanadactylus" spixi* from the Early Cretaceous Santana Formation of Brazil is also dsungaripterid. However, the characters cited are found in other pterodactyloids including tapejarids and azhdarchids (UNWIN & LÜ, submitted) and this form is possibly a tapejarid (KELLNER & CAMPOS, 1992).

The wing-phalange from Gifu compares closely in size and shape to the first and second wing-phalanges of *Noripterus*, a relatively small dsungaripterid from Xinjiang Province, China (YOUNG, 1973). Wing-phalanges of other dsungaripterids are larger, but otherwise also compare very well to the Gifu specimen. Size is not a reliable criterion for taxonomic assignments, particularly in this case, since it is not clear whether this remain is from an adult, sub-adult or juvenile. Thus, while the phalange from Shokawa exhibits dsungaripterid features (forward reflection, thick bone walls, expanded articular surfaces) there are no grounds for assigning it to any particular genus within this family. We conclude that, for the present, it should only be identified as Dsungaripteridae gen. et sp. indet.

## Discussion

Relatively thick bone walls are characteristic of dsungaripteroids (UNWIN, 1995) and possibly unique to this clade. The Shokawa specimen has an average R/t value of 2.26, which is well within the range of R/t values exhibited by terrestrial reptiles, terrestrial mammals and flightless birds (CURREY & ALEXANDER, 1985: 459). Wing bones of flying birds, with marrow-filled bones, typically have R/t values of 3.5, whereas those of flying birds with pneumatised bones exhibit R/t values ranging from 3.2 to 7.1. Typically, pterosaur wing bones have R/t values ranging from 3.0 to 10.0 (UNWIN, unpub. data), while wing elements of highly derived forms such as *Pteranodon* reach R/t values of 20 for the humerus and ulna, 10 for the radius and 7–17 for manal phalanges (CURREY & ALEXANDER, 1985: 459).

The functional significance, if any, of the relatively thick-walled wing-bones of the Shokawa pterosaur and other dsungaripteroids is unclear. This construction would reduce the risk of collapse or breakage of wing-phalanges during accidental collisions. The likelihood of collisions was probably higher for pterosaurs living in continental environments, especially cluttered habitats, than for marine pterosaurs such as *Pteranodon.* This hypothesis is consistent with the discovery of most dsungaripteroids in terrestrial deposits, but requires further study.

The discovery of a dsungaripterid in the early Early Cretaceous of Japan is not entirely unexpected. Almost all the pterosaurs so far reported from the early and mid-Early Cretaceous of central and east Asia are dsungaripterids (BAKHURINA & UNWIN, 1995), and this new record further confirms their ubiquity in this region during this time interval. We estimate that the Shokawa pterosaur had a wingspan of between 1.5 and 2 m (Fig. 5). This is relatively small compared to other dsungaripterids, but little significance can be attached to this since the ontogenetic status of this individual: juvenile, sub-adult or adult, is unknown.

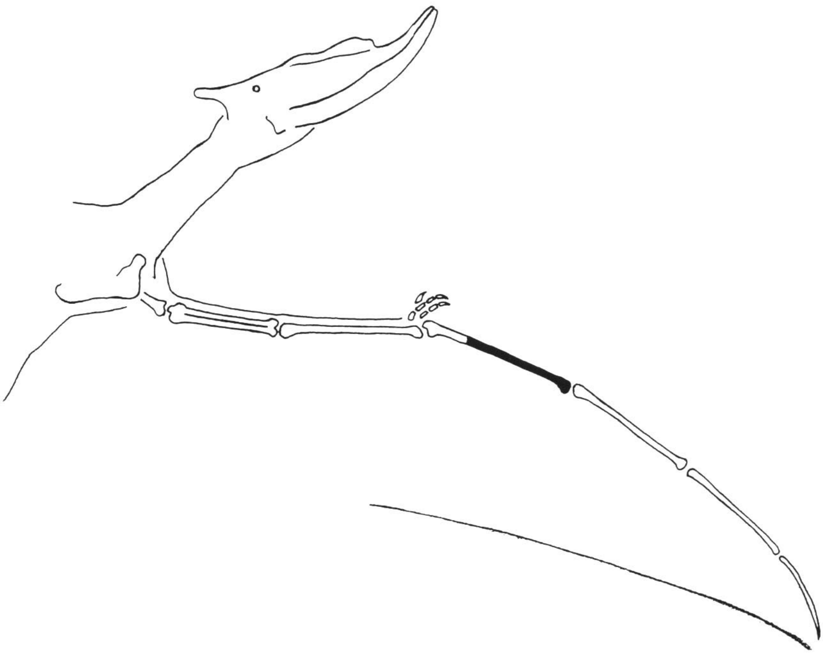

Fig. 5. The phalange superimposed on a dsungaripterid seen in ventro-lateral view.

The discovery of the Shokawa pterosaur in flood plain deposits has some interesting implications. Most pterosaurs have been recovered from marginal marine or fully marine sediments and seem to have been adapted to life in these environments (HAZLEHURST & RAYNER, 1991; WELLNHOFER, 1991). Few pterosaurs have been found in continental deposits, but the number of records is growing, especially for the Early Cretaceous. At this time, dsungaripterids seem to have been the dominant terrestrial form in Asia (BAKHURINA, 1992), an observation which is further supported by our identification of a dsungaripterid in the terrestrial deposits of Shokawa. The role of dsungaripterids within terrestrial vertebrate communities is unclear: both piscivory (BAKHURINA, 1993) and molluscivory (YOUNG, 1964) have been proposed and further work is needed to resolve this problem. At a more general level, dsungaripterids form part of an Early Cretaceous faunal association, the psittacosaur-pterosaur fauna (DONG, 1992) which was widespread across Northern China, Mongolia and, following recent discoveries at Shokawa, is now known to have extended as far east as Japan.

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